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Lymph pathways of the medial retropharyngeal lymph node in dogs

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ABSTRACT

In dogs, lymph drains from tissues throughout the head, including the tonsils, along lymphatic vessels to the facial, parotid, lateral retropharyngeal and mandibular lymph nodes. From the mandibular lymph nodes, lymph may flow to the ipsilateral medial retropharyngeal lymph nodes, or along anastomotic connections to the contralateral node. Afferent lymphatics convey lymph from these nodes to defined areas in the medial retropharyngeal nodes. They divide over the surface of the node, and within trabeculae. Terminal afferent lymphatics are connected to the subcapsular and trabecular sinuses either through circular or oval holes in the vessel wall, or terminate at the sinus where the vessel contains a valve adjacent to the point of entry. The subcapsular sinus surrounds the entire node, and is continuous with an interconnecting network of trabecular and cortical sinuses which convey lymph through the cortex. Connective tissue septa extend through the sinuses and lymph flows freely between adjacent sinuses through holes in the septal walls. Initial efferent lymphatic vessels, which arise from the medullary sinuses between medullary cords, converge towards and unite within the network of medullary trabeculae. Other vessels, which contain valve-like flaps, drain lymph from the subcapsular sinus. Efferent vessels emerge along the hilus and coalesce to form the tracheal trunk. The tracheal trunk has several layers of smooth muscle cells, well developed elastic laminae and connective tissue, surrounding the lymphatic endothelium.

Key words: Dog; lymphatic system; lymph nodes.

INTRODUCTION

The medial retropharyngeal lymph nodes in dogs receive all lymph draining from tissues throughout the head, including the tonsils (Evans, 1993). Because of their location, tonsils play a key role in initiating immune responses against antigens entering the body through the mouth or nose (Brantzaeg, 1984). Thus the lymphatic pathways associated with the medial retropharyngeal lymph nodes must play a key role in disseminating immunological information derived from the head itself as well as from ingested and inspired antigenic material.

Owing to the importance of the dog as a companion animal and as a transplantation model, its immune system has been the subject of many studies. Most of these, however, have been on the histological structure, cell populations and cell products of lymph nodes (Drinker et al. 1934; Fujita et al. 1972; Fossum & Ford, 1985) and little information is available on the lymphatic pathways associated with its lymph nodes. Some information on lymphatic pathways of lymph nodes is available from sheep (Heath & Brandon, 1983), pigs (Spalding & Heath, 1987), horses (Nikles & Heath, 1992) and rodents (Kurokawa & Ogata, 1989; Sainte-Marie et al. 1982), but the differences that exist between these species suggest that this information may not apply equally to dogs.

The aim of this study was to describe the pathways taken by lymph as it flows from tissues of the head to the medial retropharyngeal lymph node, and through the node to the tracheal trunk. These lymphatic pathways were examined using Microfil and Mercox casts, and by light and electron microscopy.

MATERIALS AND METHODS

Twenty-four greyhound dogs aged 9–24 months were used. They were sedated with acepromazine (Promex 2 or Promex 10, Apex Laboratories, St Marys, New

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South Wales, Australia) and anaesthetised with pentobarbitone sodium (Nembutal, Boehringer Ingelheim, Artarmon, New South Wales, Australia) given intravenously. None of the dogs regained consciousness; they were all killed either by exsanguination or with an overdose of pentobarbitone sodium (Lethabarb, Arnolds, Reading, Peakhurst, New South Wales, Australia).

In 9 of the anaesthetised dogs, the jugular vein was partly occluded for 9–20 min to increase the capillary pressure and promote lymph formation, and the tracheal trunk was ligated to distend the lymph pathways of the head. The lymphatic pathways were traced by dissection.

Lymph drainage to the superficial lymph nodes of the head was investigated by injecting 0.1–0.4 ml of Evans blue dye through a 30 G needle placed immediately below the skin in the area drained by the lymph node or into the parenchyma of the palatine tonsil. In some cases, Microfil (Flow Tek Inc., Boulder, Colorado, USA), a synthetic rubber compound, was injected into the palatine tonsil or through a polyethylene cannula (Dural Plastics & Engineering, Auburn, New South Wales, Australia) into an afferent lymphatic vessel.

The medial retropharyngeal lymph nodes were prepared for light microscopy and electron microscopy by injecting heparinised saline followed by fixative (4% paraformaldehyde and 2.5% glutaraldehyde in 0.067 M sodium cacodylate buffer, pH 7.2), into an afferent lymphatic at 0.2–0.3 ml/min over 5–10 min. The nodes were removed and immersed in the same fixative for a further 24 h then washed and stored in 0.1 M sodium cacodylate buffer (pH 7.2).

Segments of tracheal trunk from 4 dogs were fixed by perfusion of fixative (2.5% glutaraldehyde and 4% paraformaldehyde, pH 7.2) through the lumen. The lymphatic vessels were removed and immersed in the same fixative for a further 24 h then washed and stored in 0.1 M sodium cacodylate buffer (pH 7.2). Tissue was then prepared for transmission electron microscopy.

Sections for light and scanning electron microscopy were dehydrated in ethanol, cleared in xylol and mounted in wax. Histological sections (7 μm), stained with haematoxylin and eosin, were photographed using an Olympus BH-2 microscope with an Olympus PM-10AD/OM-2 photographic system.

Tissue blocks for scanning electron microscopy were then dewaxed, washed and dehydrated with ethanol, dried by the critical point method, sputtered with gold and examined with a JEOL 6400F scanning electron microscope.

Tissue for transmission electron microscopy was post-fixed in 1% osmium tetroxide and stained in 5% uranyl acetate, then embedded in Epon/Araldite resin. Ultrathin sections were stained with uranyl acetate followed by lead citrate and examined with a Zeiss 10C electron microscope.

Casts of lymph sinuses within the lymph node were made by injecting 0.1–0.3 ml of Mercox (CL-2B, Japan Vilene Hospital, Tokyo) or 0.3–1.0 ml Microfil through a cannula placed in an afferent lymphatic.

Microfil casts were allowed to set then the lymph nodes were dissected from the carcass and placed into fixative for 8–12 h. The preparations were then dehydrated in ethanol and cleared in methyl salicylate. They were photographed using an Olympus OM-2 bellows system. Histological sections were prepared from some nodes to confirm the identity of cleared tissues.

Lymph nodes containing Mercox casts were not disturbed for 1–2 h. They were then dissected from the carcass and placed in water at 60 °C for 8–12 h, then immersed in several changes of 15% sodium hydroxide. The casts were washed in distilled water and ethanol then air-dried. They were sputter-coated with chromium and examined with a JEOL 6400F scanning electron microscope at 3–3.5 kV.

RESULTS

Pathways of lymph flow to the medial retropharyngeal lymph node

The retropharyngeal lymph centre may consist of both medial and lateral retropharyngeal lymph nodes (Schummer & Nickel, 1979) but in 24 dogs dissected the lateral lymph lymph nodes were present in only 2. The medial retropharyngeal lymph node lay dorsolaterally on the pharynx, caudal to the digastric muscle and ventromedial to the wing of the atlas. In half the cases, there was only one node, about $36 \times 12 \times 20$ mm, which was rounded cranially and had a pointed caudal extremity. However, in the other cases, small accessory nodes, about $4 \times 8 \times 3$ mm, were present, or the lymph centre appeared to consist of partly fused node anlages, each about $16 \times 9 \times 7$ mm.

This node received primary lymph from the tissues (including tonsils) of the head (Evans, 1993) and lymph that had already passed through other lymph nodes: the parotid and mandibular and, when present, the lateral retropharyngeal and facial nodes (Fig. 1). The location of these lymphoid tissues has been described (Evans, 1993); this paper is concerned primarily with the pathways of lymph flow.

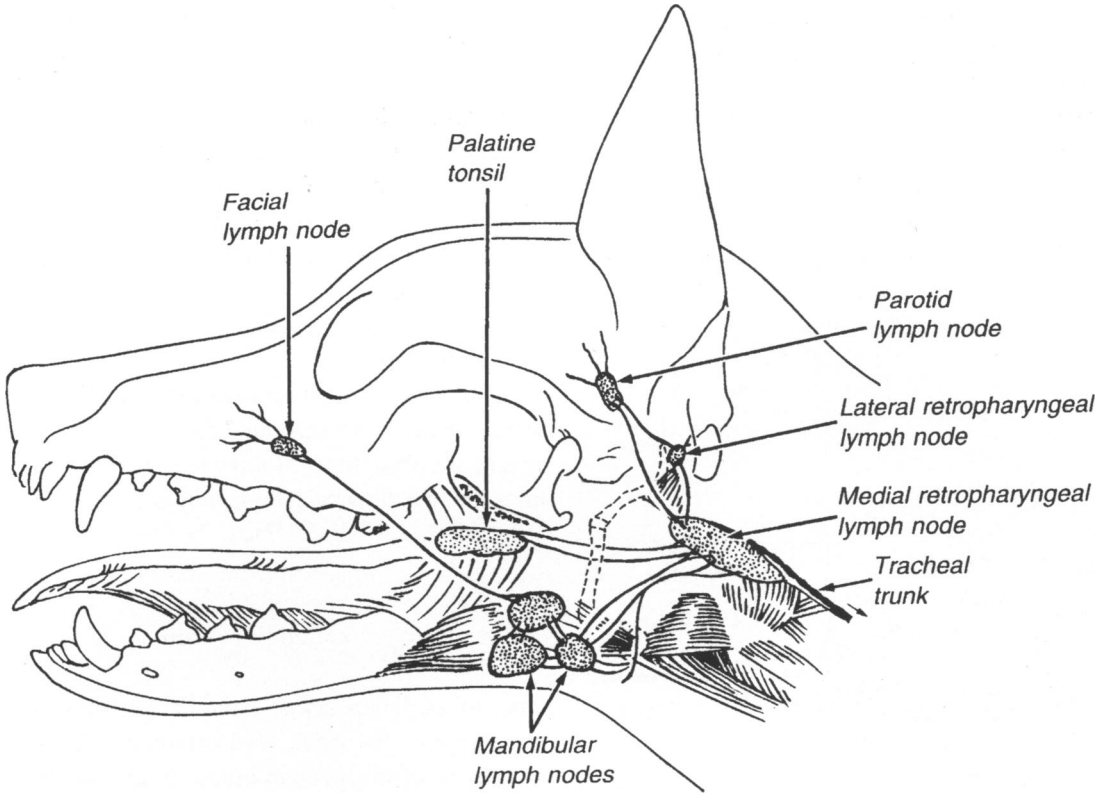


Fig. 1. Stylised diagram of a dissection of the head of a dog showing the position of lymph nodes and their lymphatic drainage to the medial retropharyngeal node and tracheal trunk.

Table. *Afferent lymph pathways to the medial retropharyngeal lymph nodes in the dog*

Origin of afferents	No. of afferents	Termination on medial retropharyngeal node
Mandibular nodes		
Ipsilateral	2–4	Middle and caudal ventrolateral
Contralateral	4–6	Middle and caudal ventrolateral
Parotid node	1–2	Craniolateral
Palatine tonsil	2–3	Ventromedial

The parotid lymph node, at the rostral border of the base of the ear, yielded 1 or 2 efferent vessels and these formed afferents to the medial retropharyngeal lymph node. The mandibular lymph centre consisted of 2 or 3 oval lymph nodes, lying subcutaneously near the angle of the jaw. The more dorsal of these, which was dorsal to the confluence of the lingual and facial veins, received lymph from the lateral surface of the head, and from the facial node, when present. Lymph from this mandibular node then flowed through interconnecting vessels to other nodes of that lymph centre (Fig. 1).

Efferent vessels from the mandibular lymph nodes followed 2 pathways. In one pathway up to 10 lymphatics emerged from the dorsal surface of the mandibular nodes, coalesced after 20–30 mm forming 2–4 collecting lymphatics, and these delivered lymph to the ipsilateral medial retropharyngeal node (Fig. 1). In the 2nd pathway 4–6 efferent lymphatics coursed ventrally and formed a plexus over the ventral surface of the pharynx before joining the efferent lymphatics from the contralateral mandibular node, and draining to the contralateral medial retropharyngeal node.

The facial node was present in only 4 of the 24 dogs, and in each of these dogs it was bilateral. It was 8–10 mm long, flattened and oval, and lay adjacent to the confluence of the superior labial and facial veins. Efferent vessels from this node followed the ventral edge of the masseter muscle to the dorsal node of the mandibular lymph centre.

The palatine tonsil, which is the largest of the tonsils in the dog, yielded 50 or more efferent vessels. They coursed around and between lobules of the adjacent minor salivary glands, then united to form 2–3 vessels which emerged near the caudal hilar region of the tonsil. These passed between the hyoid apparatus and the abluminal surface of the pharynx to reach the medial retropharyngeal node (Fig. 1).

Afferent lymph pathways to the medial retropharyngeal lymph nodes

The lymphatic vessels from the palatine tonsils and primary lymph nodes of the head converged as they

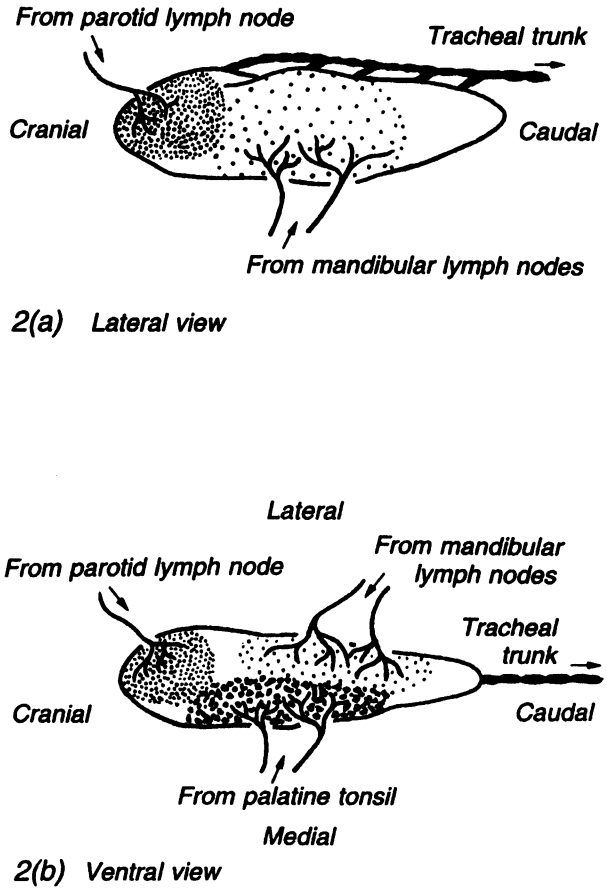


Fig. 2. Stylised diagram of the medial retropharyngeal lymph node, showing the distribution of Evans blue dye after 0.1–0.4 ml of a 1% solution was injected into afferent lymphatics to the mandibular and parotid lymph nodes, or directly into the lymphoid parenchyma of the palatine tonsil.

approached the medial retropharyngeal nodes, and they each terminated on the region of that node as set out in the Table and in Figure 2.

Afferent lymphatics divided progressively either in the perinodal fat, on the node surface, or within the capsule (Fig. 3). Furthermore, about 40% of them penetrated into the node within trabeculae before dividing to form terminal lymphatics. In all, up to 1400 terminal lymphatics delivered lymph either to the subcapsular sinus or to trabecular sinuses deeper within the node.

The terminal lymphatics, which were up to 70 μm across and within the capsule or trabeculum, were connected to the adjacent sinus in one of two ways: either through circular or oval holes, 5–10 μm across, in the vessel wall (Fig. 4), or by terminating at the sinus. In this case, a valve was present adjacent to the point of entry, which often centred over the apex of a follicle (Fig. 5).

Trabeculae, together with connective tissue septa, provided a skeletal framework for the node, and formed a branching, interconnecting meshwork which appeared to divide the node into more-or-less separate regions.

The trabeculae, which provided a protective conduit for penetrating afferent lymphatics, extended from the capsule into the lymphoid parenchyma. They were up to 300 μm wide at their origin from the capsule, and they penetrated up to 3 mm into the node. Up to 3 afferent lymphatics were present within each trabeculum, and they delivered lymph to the deep cortex (Fig. 6).

Connective tissue septa formed plate-like divisions which extended through the sinuses. However, rounded holes, up to 20 μm across, in the septal walls, allowed free flow of lymph between adjacent sinuses (Fig. 7).

Lymph sinuses

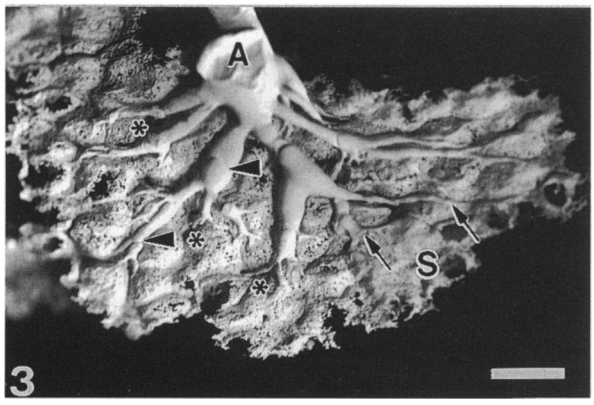
The subcapsular sinus extended around the entire periphery of the node, and was continuous between adjacent regions through holes within the septal walls. Although most of the sinus was traversed by a network of reticular cells and processes, processes were often sparse where afferent lymphatics entered the sinus, and adjacent to the surface of superficially placed follicles (Fig. 6).

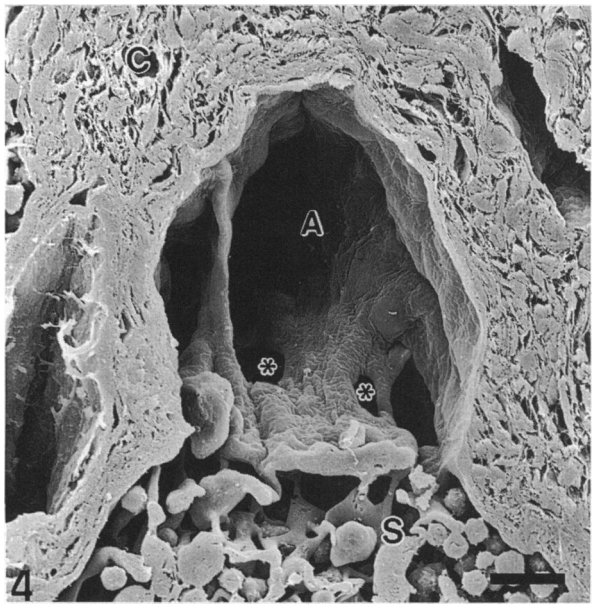
Lymph flowed through the cortex in an interconnecting network of sinuses: the trabecular, and the cortical sinuses.

Trabecular sinuses, pervaded by a reticular network, surrounded the trabeculae and septa, and were continuous with the subcapsular, cortical and medullary sinuses.

The cortical sinuses appeared in 2 forms. Some were circular or oval in cross-section and 10–45 μm across. These were seen mainly in the superficial cortex, often forming networks around the base of follicles (Fig. 8). They had a continuous lining and occasional bridging processes (1–3 μm across), but few reticular cell processes crossed their lumen (Fig. 9). The other cortical sinuses were generally larger, 20–115 μm across, and were traversed by a complex reticular network (Fig. 10). These appeared mainly in the deep cortex, where they were often located close to the high-endothelial venules. The wall was punctuated by holes, 2–3.5 μm across, through which cells appeared to migrate (Fig. 10).

The cortical and trabecular sinuses, and the subcapsular sinus over the medulla, were continuous with the medullary sinuses. These extended between the medullary cords, but in some cases appeared to be





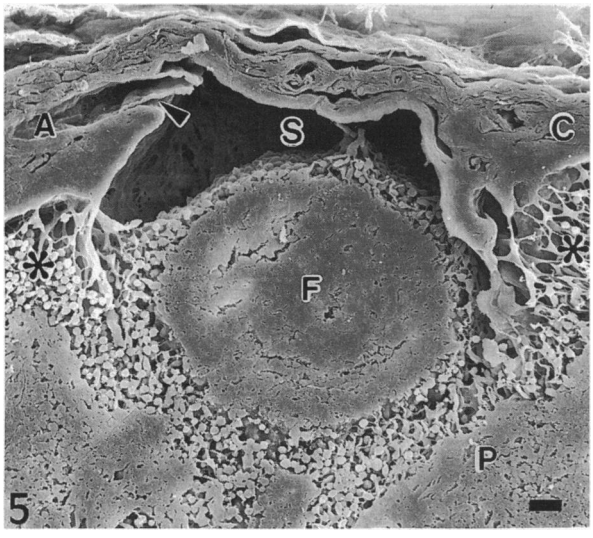


Fig. 3. Photograph of a Microfil cast of the ventrolateral surface of a medial retropharyngeal lymph node showing an afferent lymphatic (A) dividing progressively to give rise to many branches which radiate over the surface of the node. Some terminal afferent vessels are continuous with the subcapsular sinus (small arrows); other terminal vessels penetrate into the node (asterisk). Valves (large arrows) can be seen in large branches and within small terminal branches. S, subcapsular sinus. Bar, 1000 μm.

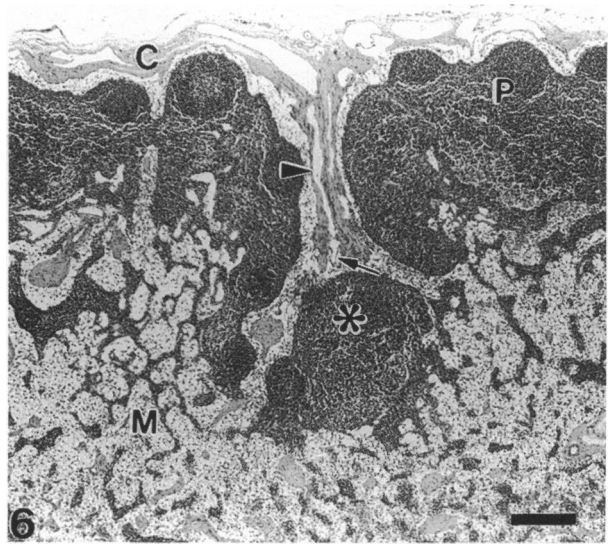


Fig. 6. Light micrograph of a transverse section, stained with haematoxylin and eosin, from a medial retropharyngeal lymph node. A penetrating afferent lymphatic (arrowhead) within a trabeculum delivers lymph to the deep cortical tissue (asterisk). A valve (small arrow) can be seen near the terminal region. P, cortical parenchyma; M, medullary tissue; C, capsule. Bar, 500 μm.

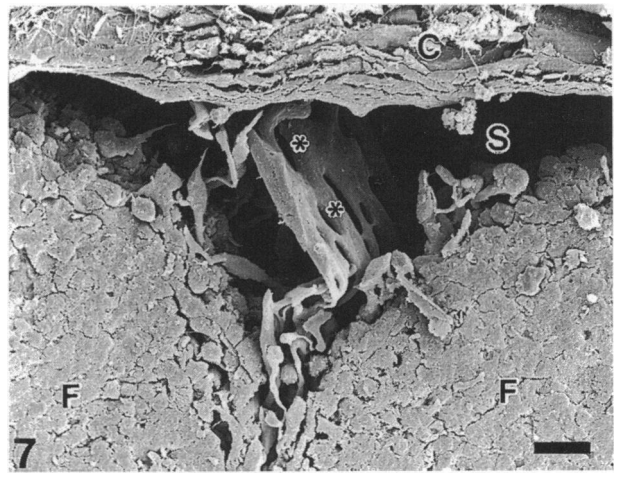
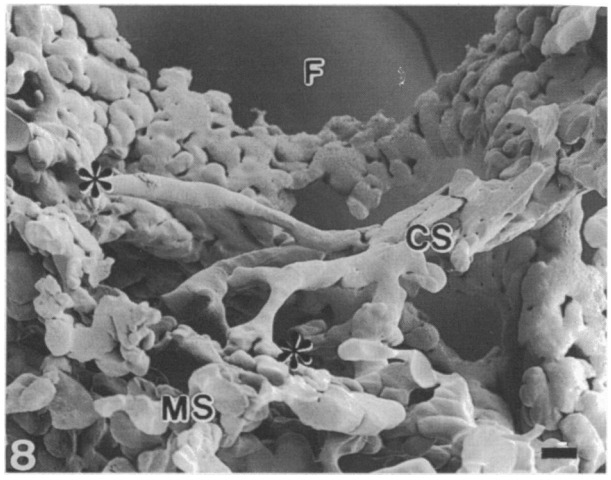
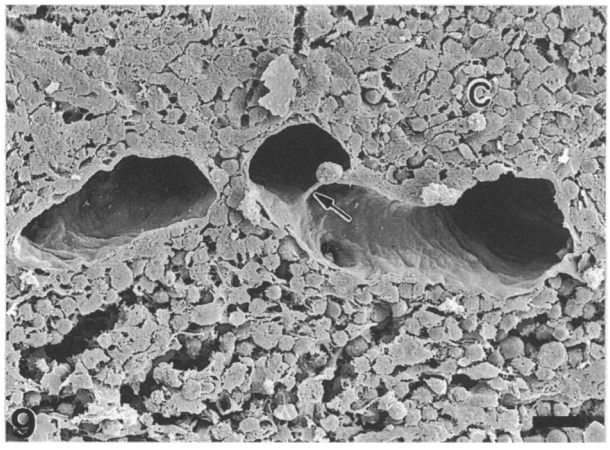


Fig. 7. Scanning electron micrograph of a septum crossing the subcapsular sinus (S) and passing between 2 follicles (F). Holes (asterisk) allow the free flow of lymph between adjacent regions of sinus. C, capsule. Bar, 10 μm.

Fig. 4. Scanning electron micrograph of a terminal afferent vessel (A) connecting with the subcapsular sinus through holes in the vessel wall (asterisks). C, capsule; S, subcapsular sinus. Bar, 10 μm.

Fig. 5. Scanning electron micrograph of a terminal afferent lymphatic (A) coursing within the capsule of the node and entering the subcapsular sinus (S) adjacent to a lymphoid follicle (F). A valve (arrowhead) can be seen at the point of entry to the subcapsular sinus. The area of the subcapsular sinus lacks the usual complex reticular network which can be seen in adjacent regions of the sinus (asterisk). P, cortical parenchyma. Bar, 20 μm.





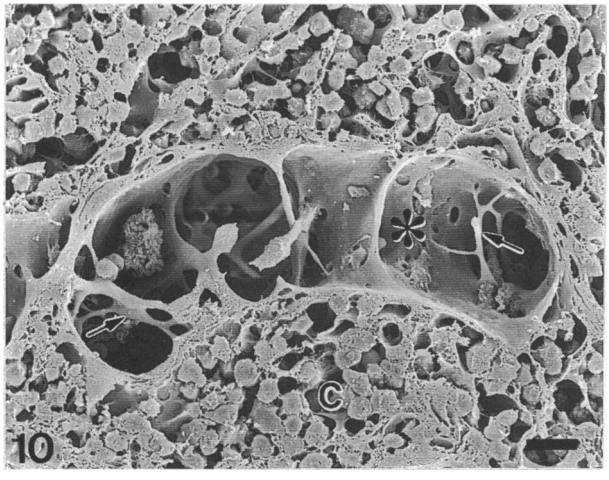


Fig. 8. Scanning electron micrograph of a fractured Mercox cast showing part of a cortical sinus network (CS) towards the base of the space previously occupied by a follicle (F). The cortical sinuses are connected (asterisk) with medullary sinuses (MS). Bar, 20 μm.

Fig. 9. Scanning electron micrograph of a cortical sinus with a smooth endothelial lining and an occasional reticular cell process (arrow) traversing the sinus lumen. C, cortical parenchyma. Bar, 10 μm.

Fig. 10. Scanning electron micrograph of a cortical sinus which is traversed by a complex network of luminal stellate cell processes (arrows). Lymphoid cells are seen migrating through holes in the sinus lining (asterisk). C, cortical parenchyma. bar, 10 μm.

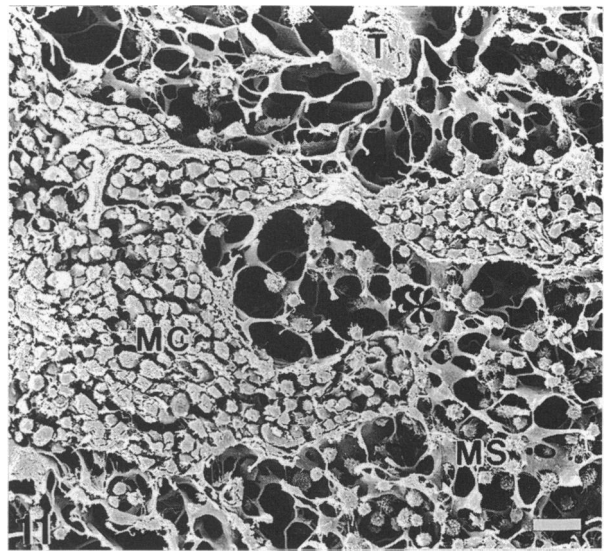


Fig. 11. Scanning electron micrograph showing a medullary sinus (MS) which surrounds and extends into (asterisk) a medullary cord (MC). T, trabeculum. Bar, 10 μm.

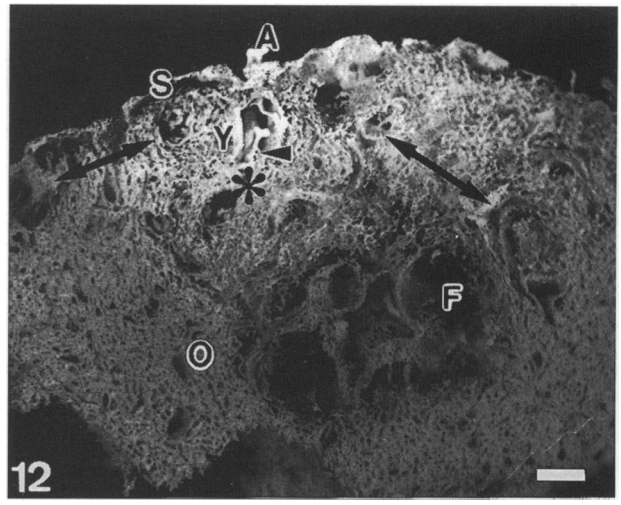
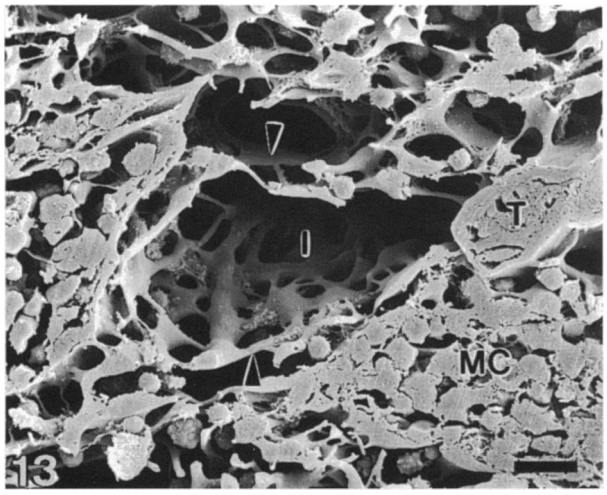


Fig. 12. Photograph of the cut surface of a Microfil cast of a medial retropharyngeal lymph node. Yellow (Y) and orange (O) Microfil had been injected into lymphatic vessels which drain the palatine tonsil (yellow) and the mandibular lymph nodes (orange). Mixing of colours occurred in adjacent regions of the subcapsular sinus (S) and within cortical and medullary sinuses (double-headed arrows). Terminal afferent vessels (arrowhead) branching from a penetrating afferent lymphatic (A) allow yellow Microfil to reach deep regions of the node (asterisk) where it almost immediately intermingles with orange Microfil. F, space occupied by a follicle. Bar, 1000 μm.

enveloped by the cords (Fig. 11). The medullary sinuses were traversed by a dense network of processes which extended from the sinus lining cells surrounding the medullary cords. Mononuclear cells were sometimes seen protruding through gaps in the sinus wall.

Microfil of different colours, injected into lymphatics derived from different primary nodes or the



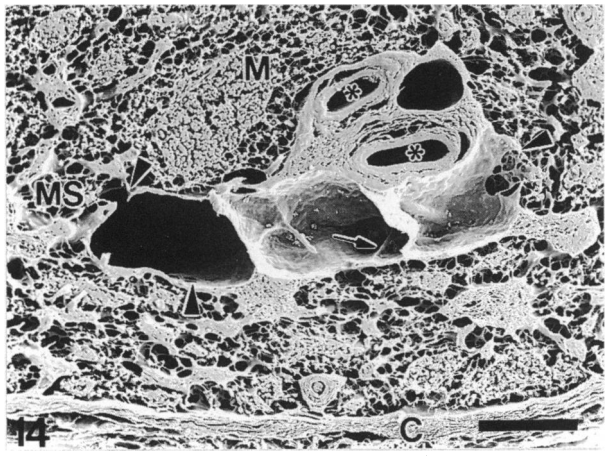
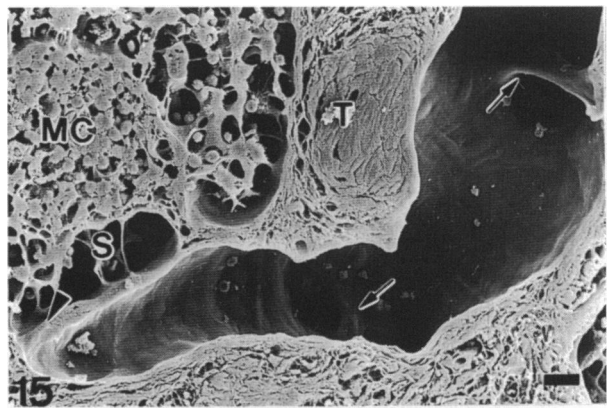


Fig. 13. Scanning electron micrograph of an initial efferent lymphatic (I) within a medullary sinus. The walls are formed by reticular cell processes (arrowheads). T, trabeculum; MC, medullary cord. Bar, 10 μm.

Fig. 14. Scanning electron micrograph of efferent lymphatics forming collecting vessels within a trabeculum. Efferent vessels are continuous with the medullary sinus (MS) through holes in the vessel wall (arrowheads). Medullary tissue (M) completely surrounds the trabeculum. C, capsule; small arrow, valve; asterisk, blood vessels. Bar, 100 μm.



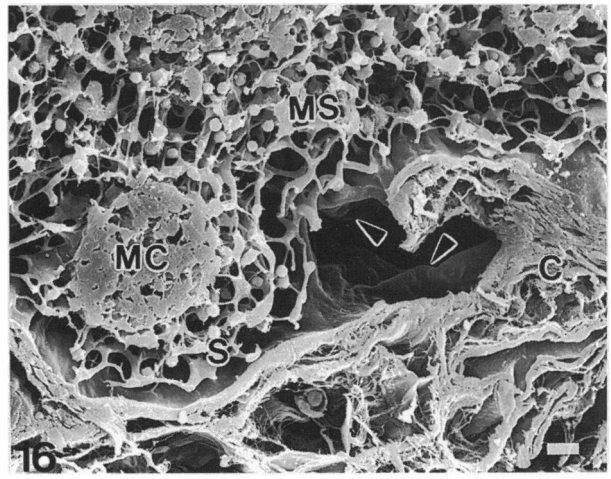


Fig. 15. Scanning electron micrograph of an efferent lymphatic within a trabeculum (T). A narrowed aperture (arrowhead) connects the lumen of the vessel with the surrounding sinus (S). Luminal processes (arrows) occur near the entry of efferent vessels. MC, medullary cord. Bar, 10 μm.

Fig. 16. Scanning electron micrograph of initial efferent draining from the subcapsular sinus (S) and medullary sinus (MS) surrounding a medullary cord (MC). Valve-like flaps (arrowheads) can be seen near the entrance to the efferent vessel. C, capsule. Bar, 10 μm.

palatine tonsil, mixed at the periphery of adjacent regions of the subcapsular sinus, within the trabecular sinuses and the cortical and medullary sinuses (Fig. 12).

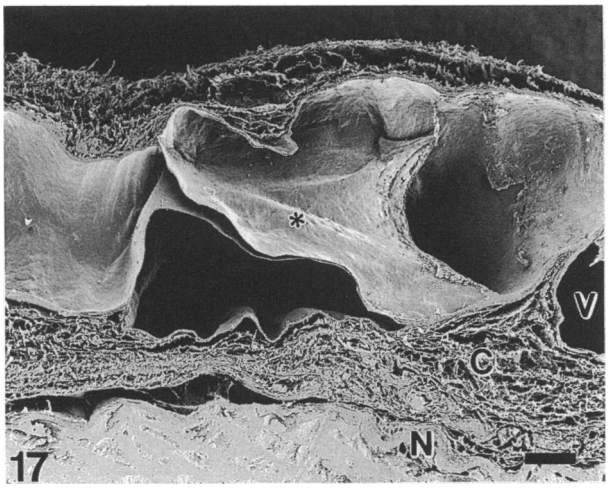
Efferent lymph pathways

Initial efferent lymphatic vessels drained from the medullary sinuses, and from the subcapsular sinus adjacent to the medulla.

The vessels which drained from medullary sinuses were 20–50 μm across, and at their origin the walls were formed by cross-linking between reticular cell processes, mostly 2.5–7.5 μm across (Fig. 13). As the vessels passed towards the trabeculae their walls progressively became more complete, although they were penetrated by holes, 10–30 μm across (Fig. 14). Within these trabeculae, these vessels joined collecting vessels which were surrounded by a single layer of smooth muscle cells abluminally. They contained few luminal processes, except near the entry of initial efferent vessels (Fig. 15). However, vessels as small as 30 μm across contained valves.

Collecting vessels coalesced within the network of trabeculae (Fig. 14) and up to 10 efferent vessels emerged from a hilar depression. This was located along the lesser curvature over the dorsocaudal surface of the node.

Initial efferent lymphatic vessels which arose at the subcapsular sinus overlying medullary cords were continuous with the sinus through valve-like openings and joined the efferent lymphatics (Fig. 16). The



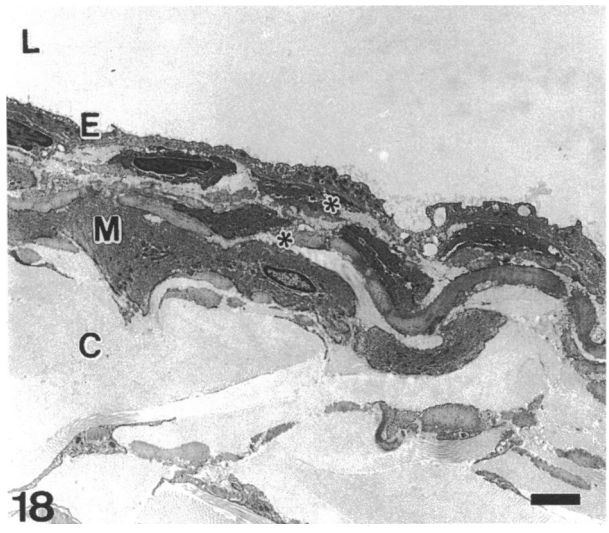


Fig. 17. Scanning electron micrograph of a tracheal lymphatic trunk over the medial retropharyngeal lymph node showing a valve (asterisk) within its lumen. The connective tissue investment (C) surrounding the vessel is closely associated with the connective tissue of the node (N) and offers protection and support to the lymphatic trunk as it receives other lymphatic vessels (V) along its course over the dorsal surface of the node. Bar, 100 μm.

Fig. 18. Transmission electron micrograph of the wall of a tracheal lymphatic trunk. Smooth muscle cells (M) are closely associated with the endothelium (E) and form several layers parallel to the vessel lumen (L). Bundles of elastic fibres (asterisk) are prominent within these layers and adjacent to the abluminal endothelial surface. C, collagen bundles. Bar, 20 μm.

efferent lymphatics sometimes formed a plexus at the hilar depression, but united in the cranial one-third of the neck to form the tracheal trunk.

The tracheal trunk, which contained valves approximately 1.5–2 mm apart (Fig. 17), lay within the deep cervical fascia and accompanied the common carotid artery and vagosympathetic trunk. The lymphatic trunk was lined by a continuous layer of endothelium (Figs 17, 18). Elastic fibres, arranged into prominent bundles, were interposed between the endothelium and the several layers of smooth muscle cells, and sometimes appeared to form almost complete laminae. Bundles of collagen fibres and fibroblasts formed the outer border (Fig. 18).

DISCUSSION

Lymph from the facial, parotid and mandibular lymph nodes, and the palatine tonsils, flows along lymphatic vessels to the retropharyngeal lymph nodes. It then traverses a network of sinuses in the cortex and medulla and is conveyed along efferent vessels to reach the tracheal trunk.

Much of the lymph reaching the medial retropharyngeal lymph node has traversed at least one, but often several nodes, and may be derived from both ipsilateral and contralateral sides. In addition, mixing of lymph occurs along this pathway, so that immunological information may be widely redistributed among the nodes. For example, lymph draining from the nasal region to the facial node mixes in the mandibular node with lymph received from other drainage sites; lymph flows between mandibular nodes and freely mixes in the adjacent efferent vessels; and lymph flowing from contralateral mandibular nodes along anastomotic lymphatic connections intermingles before entering the medial retropharyngeal node. Evidence from sheep indicates that lymphocytes, received from a preceding node along the lymph pathway, are redistributed throughout the nodal parenchyma allowing the immune response to be further potentiated (Fahy, 1980; Fahy et al. 1980).

Our observations do not support the concept of physiological compartmentalisation of lymphoid tissue and of pathways of lymph flow within the node which appears to occur in rats (Sainte-Marie et al. 1982), rabbits (Kelly, 1975) and more generally in the node anlagen of the pig (Spalding & Heath, 1987), but not in the sheep (Heath & Spalding, 1987) or horse (Nikles & Heath, 1992).

In the dog, lymphatic vessels which convey lymph from the primary lymph tissues of the head to the medial retropharyngeal lymph node terminate over defined parts of the surface of the node. Close to the node each afferent lymphatic divides, radiating over the surface of the node to form numerous terminal afferent vessels. Some enter the subcapsular sinus directly, but many penetrate into the node and deliver lymph deep within the node. In the rat a single afferent lymphatic delivers lymph to a discrete cortical unit (Sainte-Marie et al. 1982), but in the sheep and horse the lymph is widely distributed over a large area of nodal tissue (Heath & Spalding, 1987; Nikles & Heath, 1992). Although in dog nodes each terminal

afferent lymphatic enters over the apex of a follicle, as in rat nodes (Sainte-Marie et al. 1982), they differ from other species as many more terminal vessels are derived from a single afferent lymphatic. Therefore, lymph entering the node from an afferent lymphatic in dogs is associated with a relatively larger area of cortical tissue than in rats.

The subscapsular sinus extends completely around the node and is continuous with trabecular sinuses. The reticular network is extensive except where terminal afferent lymphatics enter the sinus over secondary follicles. Follicles, both in the superficial cortex and deeper in the node, are adjacent to sinuses over much of their surfaces. Antigenic material and cells carried in the lymph may be widely distributed within the sinuses before encountering phagocytic and nonphagocytic cells enmeshed in the reticular network of the sinuses, and being transported to follicles (Szakal et al. 1983; Tew et al. 1984).

Large trabeculae and septa, each surrounded by an invagination of the subcapsular or medullary sinuses, penetrate into, and extensively divide, the parenchyma. Although septa have been previously described in rat nodes, discontinuities and holes in the septal wall were not observed (Sainte-Marie et al. 1982). Despite describing division of the cortical tissue into separate physiological units, Sainte-Marie et al. (1982) did not consider septal plates to interrupt the subcapsular sinus or the pathway of lymph flow, or to contribute to morphological division of the node. In this dog lymph node, unlike those of rats, adjacent regions of sinus are continuous with one another through holes in the septa, allowing free flow of lymph.

A network of tubular sinuses conveys lymph from the subcapsular and trabecular sinuses, throughout the cortical parenchyma, to the medullary sinuses. Although cortical sinuses have been documented in a number of species including rodents (Söderström & Stenström, 1969; Kelly, 1975; Kurokawa & Ogata, 1980), ruminants (Heath et al., 1986; Heath & Spalding, 1987; Nicander et al. 1991) and horses (Nikles & Heath, 1992) similar sinuses have not been previously described in canine lymph nodes.

The complexity of the cortical sinus labyrinth resembles that which occurs in horse nodes (Heath & Nikles, 1991; Nikles & Heath, 1992). Such complex arrangements have not been described in sheep (Heath & Spalding, 1987) or rodents (Sainte-Marie et al. 1982).

Connections between the cortical sinuses and the trabecular, and less frequently, the subcapsular sinuses have been reported by Heath et al. (1986, 1987) in sheep and horses (Nikles & Heath, 1992). However, in contrast, Nicander et al. (1991) concluded from their studies in ruminants that only a few channels connecting with trabecular sinuses could exist, and that 'blind' channels occur more commonly. In the dog, pathways exist for lymph to flow freely from trabecular sinuses into cortical sinuses. These pathways do not form indirect communications as suggested by Sainte-Marie & Peng (1986).

The rapid passage of particulate matter (Nicander et al. 1991) and free movement of Microfil along cortical sinuses suggests that these sinuses are important conduits for lymph from the subcapsular and trabecular sinuses to flow through the cortical parenchyma. Some of these are located close to high endothelial venules and may provide a pathway for lymphocytes to migrate from high endothelial venules towards the base of follicles (Nieuwenhuis & Ford, 1976).

The presence of antigen within a lymph node dramatically increases the rate of lymphocyte migration across high endothelial venules (Anderson & Anderson, 1975; Hay & Hobbs, 1977; Herman, 1980) and has been associated with the appearance of 'cellular aggregates' in cortical sinuses (Anderson & Anderson, 1975). In addition, antigen may affect the pressure within the lymph sinuses and vessels to produce morphological changes within the lymph sinuses (Spalding & Heath, 1991).

Because of the close proximity of cortical sinuses to high endothelial venules, antigen trapped by cells in these sinuses would be well placed to interact with incoming lymphocytes. In this way, the transport of antigenic material, cells and cytokines to this area may play an important role in the processes of lymphocyte recruitment and selective retention of antigen-specific lymphocytes which occurs during an immune response, and in the amplification and propagation of immune responses (Fossum & Ford, 1985).

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